Fisheries and Oceans Canada | Pêches et Océans Canada
Science | Sciences

CSAS | SCCS

Canadian Science Advisory Secretariat | Secrétariat canadien de consultation scientifique

Research Document 2005/042 | Document de recherche 2005/042

Not to be cited without permission of the authors * | Ne pas citer sans autorisation des auteurs *

Linking prey and population dynamics: did food limitation cause recent declines of 'resident' killer whales (*Orcinus orca*) in British Columbia?

Disponibilité des proies et dynamique des populations : est-ce que la limitation des ressources alimentaires a pu causer les diminutions récentes des épaulards « résidants » (*Orcinus orca*) en Colombie-Britannique?

John K.B. Ford, Graeme M. Ellis, Peter F. Olesiuk

Fisheries & Oceans Canada
Pacific Biological Station
3190 Hammond Bay Road
Nanaimo, BC
V9T 6N7

* This series documents the scientific basis for the evaluation of fisheries resources in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

* La présente série documente les bases scientifiques des évaluations des ressources halieutiques du Canada. Elle traite des problèmes courants selon les échéanciers dictés. Les documents qu'elle contient ne doivent pas être considérés comme des énoncés définitifs sur les sujets traités, mais plutôt comme des rapports d'étape sur les études en cours.

Research documents are produced in the official language in which they are provided to the Secretariat.

Les documents de recherche sont publiés dans la langue officielle utilisée dans le manuscrit envoyé au Secrétariat.

This document is available on the Internet at: | Ce document est disponible sur l'Internet à:
http://www.dfo-mpo.gc.ca/csas/

ISSN 1499-3848 (Printed / Imprimé)
© Her Majesty the Queen in Right of Canada, 2005
© Sa majesté la Reine, Chef du Canada, 2005
Canada

105-06902/

ABSTRACT

Two populations of fish-eating killer whales (*Orcinus orca*) in British Columbia, known as *residents*, are listed under the Canadian Species-at-Risk Act due to their small population size and recent unexplained declines in abundance. Threats considered to potentially affect survival and recovery of these populations include environmental pollutants, physical and acoustic disturbance, and reductions in the availability or quality of salmonids, their primary prey. Recent studies have shown that chinook salmon and, to a lesser degree, chum salmon, are important prey for resident killer whales, but other smaller salmonid species are not. In this report, we assess whether food limitation was potentially a significant factor in recent declines of these whale populations. We examined the relationship between trends in killer whale population dynamics based on long-term photo-identification data, and abundance levels of chinook and chum salmon off the British Columbia coast over the past 25 years. Resident killer whale population productivity is regulated primarily by changes in survival. Periods of decline were primarily due to unusually high mortality rates that were experienced by all age- and sex-classes of whales and were synchronous in the socially-isolated two resident communities. Fluctuations in observed versus expected mortality rates showed a strong correlation with changes in chinook salmon abundance, but no relationship to chum salmon abundance. A sharp drop in coast-wide chinook abundance during the late 1990s was closely associated with a significant decline in resident whale survival. The whales' preference for chinook salmon is likely due to this species' relatively large size, high lipid content and, unlike other salmonids, its year-round presence in the whales' range. Resident killer whales may be especially dependent on chinook during winter, when this species is the primary salmonid available in coastal waters, and the whales may be subject to nutritional stress leading to increased mortality if the quantity and/or quality of this prey resource declines. Chinook salmon is clearly of great importance to resident killer whales, but determining whether the species is the principal factor limiting whale productivity will require on-going monitoring of both salmon and whale population trends.

RÉSUMÉ

Deux populations d'épaulards (*Orcinus orca*) piscivores, à savoir les populations *résidantes* vivant en Colombie-Britannique, sont inscrites dans la *Loi sur les espèces en péril* du Canada, en raison de la petite taille de ces populations et de récentes diminutions inexpliquées de leur abondance. Parmi les menaces susceptibles d'influencer la survie et le rétablissement de ces populations, on compte la contamination du milieu, la perturbation physique et acoustique, ainsi que les réductions de la disponibilité ou de la qualité des salmonidés, leur principale proie. Des études récentes ont démontré que le saumon quinnat et, dans une moindre mesure, le saumon kéta constituent des proies importantes pour les épaulards résidants, alors que ce n'est pas le cas d'autres espèces plus petites de salmonidés. Dans le présent rapport, nous évaluons la possibilité que des ressources alimentaires limitées aient pu constituer un facteur important lors des récentes diminutions de ces populations d'épaulards. Nous avons examiné la relation entre les tendances de la dynamique des populations d'épaulards, d'après des données à long terme de photo-identification, et les niveaux d'abondance du saumon quinnat et du saumon kéta au large de la côte de la Colombie-Britannique, au cours des 25 dernières années. La productivité de la population résidante d'épaulards est régie essentiellement par les changements des conditions de survie. Les périodes de déclin résultaient principalement de taux de mortalité anormalement élevés parmi tous les groupes d'âges et de sexe des épaulards, et se sont produites simultanément dans les deux communautés résidantes isolées l'une de l'autre. Des variations des taux de mortalité observés par rapport à ceux attendus ont indiqué une forte corrélation avec les variations d'abondance du saumon quinnat, mais aucun lien avec l'abondance du saumon kéta. Une baisse très marquée de l'abondance du saumon quinnat sur l'ensemble de la côte, à la fin des années 90, a été étroitement associée à une importante diminution du taux de survie des épaulards résidants. La préférence des épaulards pour le saumon quinnat tient probablement à la taille relativement grande de cette espèce, à son taux élevé en lipides et, contrairement à d'autres salmonidés, à sa présence toute l'année dans les aires de distribution des épaulards. Au cours de l'hiver, les épaulards résidants peuvent être particulièrement dépendants du saumon quinnat, principale espèce de salmonidé disponible dans les eaux côtières pendant cette période. En effet, les épaulards pourraient être soumis à un stress nutritionnel menant à une mortalité accrue, si la quantité ou la qualité de ces proies déclinaient. Le saumon quinnat est sans contredit d'une grande importance pour les épaulards résidants. Par conséquent, afin de déterminer si cette espèce représente le facteur de limitation principal de la productivité des épaulards, il faudra effectuer une surveillance continue des tendances démographiques à la fois des populations de saumon et des populations d'épaulards.

Introduction

Field studies undertaken in coastal waters of British Columbia since the early 1970s have described three separate ecotypes of killer whales (*Orcinus orca*) that inhabit nearshore waters of British Columbia and adjacent coastal areas of Washington State and southeast Alaska. These genetically-distinct forms, known as *residents*, *transients*, and *offshores*, are sympatric but do not mix, and differ in many aspects of their life history and ecology (Bigg et al. 1985, 1990; Ford and Ellis 1999; Baird 2000; Ford et al. 2000). Resident killer whales are the best known of the three ecotypes due to their predictable occurrence in protected inshore waters around Vancouver Island during summer and fall, where they concentrate to intercept migratory salmon (Heimlich-Boran 1986; Nichol and Shackleton 1996; Ford et al. 1998; Osborne 1999; Ford and Ellis 2005). Intensive annual studies over three decades using individual photo-identification have provided a complete registry of all members of the resident population, which has in turn yielded a detailed understanding of their social organization, life history and population dynamics (Bigg 1982; Bigg et al. 1987, 1990; Olesiuk et al. 1990; Ford et al. 2000; Olesiuk et al. 2005).

The resident killer whale ecotype found in British Columbia waters is divided into two distinct non-mixing populations, or *communities*. The *northern community*, comprised of 219 whales (2004 census), is found mostly in nearshore waters off northeastern Vancouver Island during summer and fall, though their overall range is much greater. The smaller *southern community* contained 84 whales in 2004 and is commonly seen off southeastern Vancouver Island and in Puget Sound, Washington, during summer and fall. Both resident communities, but particularly the southern community, were the focus of a live capture fishery during 1964-74, which removed an estimated 63 whales. This cropping is believed to have depleted the size and altered the sex- and age-structure of the southern resident community, and intentional shootings by fishermen and other mariners prior to the 1970s may have impacted both communities (Olesiuk et al. 1990).

From the early 1970s to the mid 1990s, the northern and southern communities grew by approximately 32% and 74%, respectively. Although there were some years of negative growth during this time, both communities showed prolonged periods of increase at nearly 2.6% per year, the maximum intrinsic growth rate (Olesiuk et al. 1990, 2005; Krahn et al. 2004). However, starting in the mid-1990s, both communities entered a period of lower productivity, with the southern community dropping 17% and the northern community 7-9% by 2001 (Krahn et al. 2004; Olesiuk et al. 2005). These unexplained declines have led to considerable concern regarding the conservation status of these small populations. In 2001, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) listed southern residents as *Endangered* and northern residents *Threatened*, due to their low and declining abundance and potential threats from habitat degradation. These listings subsequently became law under the Canadian Species at Risk Act (SARA). In the U.S., the National Marine Fisheries Service was petitioned in 2001 to list southern residents under the Endangered Species Act, which resulted in a proposed *Threatened* listing in 2004. Southern residents were declared *Depleted* under the U.S. Marine Mammal Protection Act in 2003, and *Endangered* by Washington State in 2004.

A recovery strategy for resident killer whales in Canada, as mandated by SARA, is currently in development. Since it is not known what the historical size of the resident population may have been, what the current carrying capacity of the whales' environment may be, or what factors caused the recent decline, recovery planning has taken a broad

approach. Three main categories of threats identified in the draft recovery strategy document[1] that are considered to be potentially significant are 1) environmental contaminants such as PCBs and other persistent organic pollutants, 2) physical and acoustic disturbance from vessels and other industrial activity, and 3) reductions in the availability or quality of prey. Because of uncertainty about which of these limiting factors and threats may be most important, there is currently little basis for delineating research priorities or rationalizing management actions to promote recovery.

Given that resident killer whales are top-level predators and are not currently hunted, it is likely that they are ultimately limited by bottom-up processes mediated through food limitation. Recent studies of foraging ecology of resident killer whales (Ford and Ellis 2005) indicate that the population preys mainly on salmon, particularly chinook (*Oncorhynchus tshawytscha*) and to a lesser degree chum salmon (*O. keta*). Studies on population dynamics indicate that population productivity of residents is regulated mainly by changes in survival rather than reproduction (Olesiuk et al. 2005). In this paper, we assess whether prey availability may be limiting resident killer whale populations by examining the relationship between salmon abundance and status and survival patterns of killer whales.

Results and Discussion

Killer Whale Population Trends and Population Dynamics

Population trends and measures of population dynamics of resident killer whales were derived from long-term registries of individual killer whales maintained by the Cetacean Research Program (Pacific Biological Station, Nanaimo, B.C.) for northern residents, and by the Center for Whale Research (Friday Harbor, Washington) for southern residents.

The overall population trend of northern and southern resident killer whales during 1974-2004 is illustrated in Figure 1. During the 1970s, 1980s and early 1990s, the northern resident community increased exponentially at an annual rate of 2.6% (Olesiuk et al. 2005). The population peaked in 1997, dropped 7-9% by 2001, then increased by 8% again by 2004. The southern resident community also exhibited periods of strong growth during the mid-1970s to the mid-1990s, but experienced a minor decline in the early 1980s, and a sharp decline of 17% during 1997-2001. From 2002-2004, the community increased again by 6%.

Temporal changes in survival and reproductive rates were examined by calculating the ratio of the number of deaths and births actually observed to the number expected based on our population model. The expected number of births and deaths each year was estimated by applying the sex- and age-specific mortality and fecundity schedules derived in Olesiuk et al. (2005) for a period of unrestrained growth during 1973-96 to the observed sex- and age-structure of the population in each year. The result indicates the number of births and deaths expected had animals continued to reproduce and die at the rate observed while the population was increasing exponentially. This method is preferred

[1] Killer Whale Recovery Team, Draft National Recovery Strategy for Northern and Southern Resident Killer Whales (*Orcinus orca*). Prepared for Public Consultations, Spring 2005, for Fisheries and Oceans Canada, on behalf of the Resident Killer Whale Recovery Team. 70 pp

over a simpler analysis of crude birth and death rates (the number of births or deaths divided by number of animals in the population), in that it explicitly takes into account the sex and age structure of the population. This facilitates comparison among populations or segments of it that differ in sex and age composition. This was particularly important for the southern resident community, because its sex- and age- structure had been altered just prior to the study by a live-capture fishery, and its sex- and age- structure evolved over the course of the study as it recovered. Because there was sometimes uncertainty associated with exact year of birth or death, and numbers were small, and births or deaths might be influenced by effects that were cumulative over several years (e.g. nutritional stress), we expressed the observed to expected ratios as 3-year running averages.

Examination of trends in the ratio of observed to expected mortalities of northern and southern resident communities for each year during 1979-2004[2] reveals that periods of decline in the two communities are associated with higher than expected mortalities (Fig. 2). Southern residents experienced two periods of greater than expected mortalities, the first in the early 1980s, and the second in the mid to late 1990s, separated by several years of fewer deaths than expected in the late 1980s. A similar pattern can be seen in the northern resident community, though the period of high mortality in the early 1980s is less apparent. The periods of major decline in the late 1990s, however, are clearly synchronized, resulting in a highly significant positive correlation between the mortality indices of the two communities (Fig. 3; $F_{1,26} = 5.3$, $r^2 = 0.345$, $p < 0.001$). Examination of the patterns of mortality showed that unexpectedly high death rates were not confined to particular pods or clans, but some groups showed different mortality rates than others (Appendix 1; Krahn et al. 2004). Interestingly, the first period of high mortality exhibited by the southern residents in the mid-1980s was only evident in the A-clan of the northern community (Appendix 1). Mortality patterns of northern and southern residents are shown with respect to age- and sex-classes in Figures 4 and 5, respectively. As noted by Olesiuk et al. (2005), unexpectedly high mortality rates were distributed broadly among age- and sex-classes. A survival index was thus calculated for both all sex- and age-classes in the southern and residents combined.

Although expected to be less of a determinant of population status, we also examined trends in the ratio of observed to expected births in the northern and southern resident communities during 1979-2004 are shown in Figure 6. Birth rates showed little fluctuation in northern residents during this period, though southern residents appeared to experience at least two periods with unexpectedly low birth rates, one in the early 1980s and the other in the late 1990s. No significant correlation was found between annual deviations from expected birth rates in the two resident communities ($r^2 = 0.017$, $P>0.5$). Overall, changes in birth rates varied over a narrower range than did mortalities, which were the principal factors driving the synchronous declines experienced by both northern and southern resident communities.

Resident feeding ecology and distribution

Both northern and southern resident communities have a distinct preference for chinook salmon over any other prey type during late spring through early fall (Ford et al. 1998; Ford and Ellis 2005). Their diet consists predominantly of this species during the months of May through August, in all parts of the coast that sampling has been

[2] These years were chosen because of the availability of data on prey abundance for this period.

undertaken. Chinook salmon appears to be preferred over other salmonid and non-salmonid species due to its large body size, high lipid content, and year-round availability in the whales' coastal habitat. Sockeye and pink salmon, which are abundant during migrations to spawning rivers in July-August, are not a significant prey species. For a 4-5 week period in late September and October, fall-migrating chum salmon comprises the main part of the diet of northern resident whales, though chinook is still a significant component and is likely targeted preferentially when available. Fall sampling of feeding by southern residents has not yet been undertaken, but it is likely similar to that of northern residents. Demersal, non-salmonid fishes such as lingcod and Pacific halibut are known to be consumed by resident whales from remains found in the stomach of a stranded northern resident individual and from field observations of predation. These species seem not to be significant prey during May to October, although it is possible that they represent a more important food source during winter and spring. Diet of resident whales is essentially unknown during this latter period. However, it is likely that the strong preference for chinook salmon shown by resident whales continues beyond summer and fall, and it remains the prey species of choice in all months of the year.

The distribution and movement patterns of resident killer whales are consistent with what might be expected of an animal having a year-round focus on chinook salmon as preferred prey. The known ranges of northern and southern resident communities are illustrated in Figure 7. Both communities frequent relatively well-defined 'core areas' off northeastern and southeastern Vancouver Island during summer and fall, but use of these areas falls off sharply by late October or November (Osborne 1999; Ford et al. 2000). Sightings during December to April are infrequent, partly due to low observer effort during winter and early spring, especially in remote regions. Sightings of northern residents during this period have been made in all parts of their range, but most tend to be in remote parts of the northern mainland coast of British Columbia or in southeast Alaska. Groups during winter and spring tend to be small compared to summer and fall, typically consisting of only 1 or 2 matrilines. In May and June, northern residents are found more consistently in predictable locations off the northern Queen Charlotte Islands and the central and north mainland coasts (Ford et al. 2000, Ford and Ellis, unpubl. data). These locations are also known concentration areas for early runs of chinook salmon, which are destined for rivers in the area. There is a southward shift in the occurrence of northern residents during June-July, that coincides with a similar southward shift in migratory runs of chinook salmon (Riddell 2004).

Movements of southern residents are also poorly known during December-April. One of the three southern resident pods, J pod, has been recorded in inshore waters off southern Vancouver Island and in Puget Sound during all months of the year, but periods of weeks without sightings in winter and early spring are common (Osborne 1999; Ford et al. 2000). The other two southern resident pods, K and L, usually depart for outer coast areas during the entire winter-spring period (Osborne 1999). Sightings of these pods during December-April are few in number and are scattered along the coast over a range of about 2,200 km, from Monterey Bay, California to Langara Island, near the British Columbia/Alaska border. Winter sightings in Monterey Bay coincided with the occurrence of local concentrations of chinook salmon (Krahn et al. 2004). K and L pods often return to inshore waters in early summer via Johnstone Strait off northeastern Vancouver Island, suggesting that they frequent the northern portion of their range more than the few sightings in that region might suggest (Ford et al. 2000; Ford and Ellis, unpubl. data). There is no evidence that members of either resident communities range more than 50 km from shore.

Prey Abundance

Measures of chinook abundance were derived from the Pacific Salmon Commission (PSC) Chinook Model, which uses sizes of 30 model stocks to generate abundance estimates for 6 coastal regions, shown in Figure 8. This model provides annual forecasts of chinook abundance for fisheries management, but estimates for each year are recalibrated based on actual catch and escapement data for the latest year in the series.[3] We used the average annual abundance for each of the 6 regions over the period 1979-2004 to calculate an annual index of relative abundance for each region (Figure 9).

Chinook salmon experienced a major coast-wide decline in abundance during the late 1990s. Abundance indices show that in the early 1980s, chinook abundance in different regions was quite variable, with some lower but most higher than the long-term average. By 1990, all indices were starting a declining trend that became precipitous by the mid-1990s, when the abundance in all regions was well below the long-term average. This decline was a result of poor ocean survival during several years of strong El Niño-like conditions (Pacific Scientific Advice Review Committee, Fisheries and Oceans Canada (1999–2001); B. Riddell, Pacific Biological Station, pers. comm.). The coast-wide period of low abundance continued until 2000, at which time sharp increases in abundance occurred. By 2003, all regional indices except the Strait of Georgia were above the long-term average.

Chum salmon did not experience the declines seen in chinook salmon. The abundance of chum salmon was determined from the Pacific Salmon Commission's Inner South Coast Management Area (Ryall et al. 1999, footnote[4]). The area includes chum from 400 different river and stream systems in southern British Columbia, including the large Fraser River runs. Abundance of chum salmon in this area had wide fluctuations over the period 1973-2003, but overall showed a minor increasing trend (Fig. 10).

Relationship of Population Dynamics to Prey Abundance

Trends in the survival patterns of resident killer whales were strongly related to fluctuations in the abundance of chinook salmon, but not chum salmon. Deviations in ratios of observed to expected mortalities of both resident communities combined were highly correlated to variations in overall chinook abundance indices (Fig. 11). Recognizing that changes in chinook abundance may not result in immediate effects on mortalities in the same year, various time lags were examined for their effect on the strength of the correlation (Table 1). This revealed that mortality deviations were most highly correlated to changes in chinook abundance after a lag of one year ($F_{1,26}$ = 73.9, r^2 = 0.7627, $P<0.001$) (Fig. 11). Significant relationships existed between deviations in mortalities and chinook abundance in separate coastal regions, but these correlations were generally weaker than for the coast-wide abundance index (see Appendix 2). No significant

[3] Descriptions of the PSC Chinook Model and calibration procedures are provided in Pacific Salmon Commission Joint Chinook Technical Committee Report TCChinook (97)-2, 1997, and Report TCChinook (04)-2.

[4] Pacific Salmon Commission Joint Chum Technical Committee, Final 2002-2003 Post Season Summary Report TCChum(05)-1.

relationship was found in comparisons of mortality rate deviations in northern and southern community with chum abundance over the period 1974-2004 (Fig. 12).

Coast-wide chinook abundance showed a weak but statistically significant positive correlation with birth rates of resident killer whales ($F_{1,23} = 6.77$, $r^2 = 0.227$, $P < 0.05$, Fig. 13). No significant relationship was found between resident birth rates and chum salmon abundance (Fig. 12).

Is Prey Limiting Resident Killer Whale Populations?

The strong correlation between changes in chinook salmon abundance and population dynamics of resident killer whales suggests that prey limitation may have been an important factor in recent population declines. If true, this single prey species must play a key role in the survival of resident killer whales, which seems surprising given the diversity of prey that killer whales are capable of feeding upon, plus the fact that resident killer whales are known to prey on a variety of different fish species (Ford et al. 1998; Ford and Ellis 2005). However, there are a number of reasons why resident killer whales may specialize on chinook salmon as their preferred year-round food resource, and why sudden declines in chinook availability may lead to decreased survival.

Prey choice in resident killer whales, as in other predators, is likely influenced by rates of encounters with a prey species and its profitability, which is determined by the prey item's net energy value and the amount of time needed to catch and handle it (Stephens and Krebs 1986; Scheel 1993; Bowen et al. 2002). Killer whales are the largest predators in the ocean and hunt a wide variety of vertebrate prey types, from small schooling fish to the largest of the baleen whales. Despite the broad predatory capabilities of the species, studies in different global regions indicate that populations of killer whales have high degrees of dietary specialization (Guinet 1991; Hoelzel 1991; Similä and Ugarte 1993; Guinet and Bouvier 1985; Ford et al. 1998; Visser 1999; Baird 2000; Saulitis et al. 2000; Pitman and Ensor 2003). Such specialization likely improves the profitability of feeding on particular prey types, which may require very different and elaborate cooperative foraging tactics for efficient utilization as a food resource. Foraging tactics in killer whale populations appear to be behavioural traditions that are passed across generations by mimicry and learning, a strategy made possible by the unusual long-term social stability (Bigg et al. 1990; Hoelzel 1991; Guinet and Bouvier 1995; Ford et al. 1998; Baird 2000). Foraging specializations are, along with other behavioural traditions, likely important social isolating mechanisms that lead ultimately to the evolution of genetically- and ecotypically-distinct populations that often exist in sympatry.

Prey choice in resident killer whales is probably restricted to a fairly narrow array of appropriate prey species as determined by their foraging specialization. Resident killer whales are fish specialists, particularly salmonids, and within this prey type, chinook salmon may well have the highest profitability (Ford and Ellis 2005). They are the largest of the salmonids and have the highest lipid content and energy density, which appear to be important factors in prey choice by fish-eating killer whales (Stansby 1976; Winship and Trites 2003; Ford and Ellis 2005). Unlike other salmonids in the region, many chinook populations spend their lives in coastal waters (Groot and Margolis 1991) and thus are available to the whales throughout the year. Sockeye, pink and chum salmon, which are by far the most abundant salmonids in the northeastern Pacific, have primarily oceanic distributions most of their lives, and pass through the whales' coastal habitat quickly

during summer on their migrations to spawning rivers. Migratory chinook are probably present in sufficient densities at this time to meet the whales' nutritional requirements, and sockeye and pink salmon are rarely preyed upon despite their greater abundance. In fall, migrating chum salmon, the second largest salmonid species, are abundant in coastal waters and represent a short-term prey resource for residents whales. Residents appear to maintain their preference for chinook even during the period of chum salmon abundance (Ford and Ellis 2005).

The fact that mortality patterns in the northern and southern resident communities were correlated with one another, and both showed the strongest negative correlations with overall chinook abundance along the west coast as opposed to any one area, suggests prey limitation is taking place on a large geographic scale. In late fall, resident killer whales mostly depart from their inshore 'core' areas and appear to range widely throughout outer coastal waters from November through April. Non-migratory chinook are available at this time, but apparently at densities that do not support large aggregations of whales in predictable locations, as seen in summer and fall. In years of average to high chinook abundance, there is likely sufficient food available to meet the whales' energetic needs until migratory chinook begin concentrating in spring en route to coastal spawning rivers. However, if chinook availability declines suddenly, as it did in the late 1990s, resident killer whales may well experience nutritional stress over the winter, leading to decreased population productivity. It is likely that the energy density of chinook also is reduced during years with poor ocean survival, as observed in sockeye salmon (Crossin et al. 2004), further adding to an energetic deficit. Shifting to alternative prey species such as groundfish may not be adequate to meet the energetic needs of resident killer whales, especially if these species are insufficient either in quantity or quality (Trites and Donnelly 2003).

Nutritional stress could have a range of potential lethal and sub-lethal effects on killer whales. In a recent review, Trites and Donnelly (2003) noted that nutritionally-stressed populations of pinnipeds show evidence of reduced body size, reduced birth rates, increased mortality of neonates and juveniles, modification of foraging and other behaviours, and changes in blood chemistry and body composition. Although many such responses cannot easily be assessed in wild killer whales, patterns of mortality can be evaluated for their consistency with a hypothesis of nutritional stress. During declines of both resident communities, unexpectedly high death rates were broadly distributed among different age- and sex-classes. This is in contrast to patterns evident in nutritionally-stressed pinnipeds, which show mortalities concentrated among young age-classes as result of inadequate nursing of neonates and poor foraging skills of newly-weaned, inexperienced juveniles (Trites and Donnelly 2003). Although neonatal mortality is difficult to estimate in killer whales (Olesiuk et al. 2005), there is no evidence that death rates were skewed towards juveniles or any other age- or sex-class. It is probable that this is a result of extensive food sharing and provisioning that takes place within matrilines of resident killer whales (Ford and Ellis 2005), which would tend to spread nutritional stress among group members of all ages.

Although food limitation may have played a major role in recent declines of resident killer whales, it is unlikely to have been the only factor involved. These animals carry unusually high burdens of toxic pollutants such as PCBs and PBDEs (Ross et al. 2000; Rayne et al. 2004), which may act synergistically along with inadequate nutrition to increase susceptibility to disease or other health effects during periods of low prey abundance.

Future chinook salmon returns and whale population trends will provide the ultimate test of the hypothesis that food limitation is determining killer whale productivity. Analysis of historical chinook abundance may also provide insight into longer-term productivity of resident killer whale populations, which would help to establish recovery goals. We believe that there is currently sufficient evidence to conclude that chinook play an important role in regulating killer whale populations, and that ensuring adequate abundance of chinook should be a priority in resident killer whale recovery planning.

Acknowledgements

We are very grateful to K. Balcomb, Center for Whale Research, for providing data on the status of southern resident whales. We thank K. Fraser, R. McNicol, and P. Ryall for assisting with salmonid data, and J. Cave, B. Riddell, D. Patterson, and T. Quinn for helpful discussions.

Literature Cited

Baird, R. W. 2000. The killer whale: foraging specializations and group hunting. Pages 127-153 *in* J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead, editors. Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago, IL.

Bigg, M. A. 1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. Rep. Int. Whal. Comm. **32**:655-666.

Bigg, M. A., G. M. Ellis, J. K. B. Ford, and K. C. Balcomb. 1987. Killer whales: a study of their identification, genealogy and natural history in British Columbia and Washington State. Phantom Press, Nanaimo, British Columbia.

Bigg, M. A., J. K. B. Ford, and G. M. Ellis. 1985. Two sympatric forms of killer whales off British Columbia and Washington. *in* Sixth Biennial Conf on the Biol. of Marine Mammals, November 1985, Vancouver, Canada.

Bigg, M. A., P. F. Olesiuk, G. M. Ellis, J. K. B. Ford, and K. C. Balcomb, III. 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Rep. Int. Whal. Commn. **Special Issue12**:383-405.

Felleman, F. L., J. R. Heimlich-Boran, and R. W. Osborne. 1991. The feeding ecology of killer whales (*Orcinus orca*) in the Pacific northwest. Pages 113-147 *in* K. Pryor and K. S. Norris, editors. Dolphin Societies: Discoveries and Puzzles. University of California Press, Berkeley, CA.

Ford, J. K. B. 1991. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Can. J. Zool. **69**:1454-1483.

Ford, J. K. B., and G. M. Ellis. 1999. Transients: Mammal-Hunting Killer Whales of British Columbia, Washington, and Southeastern Alaska. UBC Press and U of Washington Press, Vancouver BC and Seattle WA.

Ford, J.K.B., and G. M. Ellis. 2005. Prey selection and food sharing by fish-eating 'resident' killer whales (*Orcinus orca*) in British Columbia. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/041.

Ford, J. K. B., G. M. Ellis, and K. C. Balcomb. 2000. Killer Whales: the Natural History and Genealogy of *Orcinus orca* in the Waters of British Columbia and Washington, Second Edition. UBC Press and Univ. of Washington Press, Vancouver, BC and Seattle, WA.

Ford, J. K. B., G. M. Ellis, L. Barrett-Lennard, A. Morton, R. Palm, and K.C. Balcomb 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Can. J. Zool. **76**:1456-1471.

Groot, C., and L. Margolis, editors. 1991. Pacific salmon life histories. UBC Press, Vancouver, BC.

Guinet, C. 1991. Comportement de chasse des orques (*Orcinus orca*) autour des iles Crozet. Can. J. Zool. **70**:1656-1667.

Guinet, C., and J. Bouvier. 1995. Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. Can. J. Zool. **73**:27-33.

Healey, M. C. 1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*). Pages 313-393 *in* C. Groot and L. Margolis, editors. Pacific Salmon Life Histories. UBC Press, Vancouver, B.C.

Heimlich-Boran, J. 1986. Fishery correlations with the occurrence of killer whales in greater Puget Sound. Pages 113-131 *in* B. C. Kirkevold and J. S. Lockard, editors. Behavioral Biology of Killer Whales. Alan R. Liss, Inc., New York.

Hoelzel, A. R. 1991. Killer whale predation on marine mammals at Punta Norte, Argentina; food sharing, provisioning and foraging strategy. Behav. Ecol. Sociobiol. **29**:197-204.

Hoelzel, A. R. 1993. Foraging behaviour and social group dynamics in Puget Sound killer whales. Anim. Behav. **45**:581-591.

Krahn, M.M., M.J. Ford, W.F. Perrin, P.R. Wade, R.P. Angliss, M.B. Hanson, B.L. Taylor, G.M. Ylitalo, M.E. Dahlheim, J.E. Stein, and R.S. Waples. 2004. 2004 Status review of Southern Resident killer whales *(Orcinus orca)* under the Endangered Species Act. U.S. Dept. Commer., NOAA Tech. Memo. NMFSNWFSC-62, 73 p.

Nichol, L. M., and D. M. Shackleton. 1996. Seasonal movements and foraging behaviour of northern resident killer whales (*Orcinus orca*) in relation to the inshore distribution of salmon (*Oncorhynchus* spp.) in British Columbia. Can. J. Zool. **74**:983-991.

Olesiuk, P. F., M. A. Bigg, and G. M. Ellis. 1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Rep. Int. Whal. Comm. **Special Issue12**:209-242.

Olesiuk, P.F., G. M. Ellis, and J. K. B. Ford. 2005. Life history and population dynamics of northern resident killer whales (*Orcinus orca*) in British Columbia. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/045.

Osborne, R. W. 1999. A historical ecology of Salish Sea "resident" killer whales (*Orcinus orca*): with implications for management. University of Victoria, Victoria, BC.

Pacific Scientific Advice Review Committee, Fisheries and Oceans Canada (1999–2001) State of the Ocean Report: 1999 and 2001. www.pac.dfo-mpo.gc.ca/sci/psarc/OSRs/Ocean_SSR_f.htm

Pitman, R. L., and P. Ensor. 2003. Three forms of killer whales (*Orcinus orca*) in Antarctic waters. J. Cetacean Res. Manage. **5**:131-139.

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. UBC Press, Vancouver, BC.

Riddell, B. 2004. Pacific salmon resources in central and north coast British Columbia. Pacific Fisheries Resource Conservation Council, Vancouver, British Columbia. 156 pp.

Ryall, P., C. Murray, V. Palermo, D. Bailey, and D. Chen. 1999. Status of clockwork chum salmon stock and review of the clockwork management strategy. 99/169, Fisheries and Oceans Canada, Ottawa, ON.

Saulitis, E., C. Matkin, Barrett-Lennard, K. Heise, and G. Ellis. 2000. Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. Mar. Mamm. Sci. **16**:94-109.

Scheel, D. 1993. Profitability, encounter rates, and prey choice of African lions. Behav. Ecol. **4**:90-97.

Silber, G. K., M. W. Newcomer, and H. Perez-Cortez-M. 1990. Killer whales (*Orcinus orca*) attack and kill a Bryde's whale (*Balaenoptera edeni*). Can. J. Zool. **68**:1603-1606.

Similä, T. 1997. Sonar observations of killer whales (*Orcinus orca*) feeding on herring schools. Aquat. Mamm. **23**:4.

Similä, T., and F. Ugarte. 1993. Surface and underwater observations of cooperatively feeding killer whales in northern Norway. Can. J. Zool. **71**:1494-1499.

Stansby, M. E. 1976. Chemical characteristics of fish caught in the northeast Pacific Ocean. Mar. Fish. Rev. **38**:1-11.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey.

Visser, I. 1999. Benthic foraging on stingrays by killer whales (*Orcinus orca*) in New Zealand waters. Mar. Mamm. Sci. **15**:220-227.

Wiles, G. J. 2004. Washington State status report for the killer whales. Washington Department of Fish and Wildlife, Olympia, Washington.

Winship, A. J., and A. W. Trites. 2003. Prey consumption of Steller sea lions (*Eumetopias jubatus*) off Alaska: how much prey do they require? Fish. Bull. **101**:147-167.

Table 1. Effect of varying time lags on strength of correlation between deviations in expected resident mortality rates and overall coastal abundance of chinook salmon.

Lag (yrs)	r^2	Signif.
-2	0.0183	0.510
-1	0.1552	0.046
0	0.5089	<0.0001
1	0.7627	<0.0001
2	0.5788	<0.0001
3	0.2104	0.028
4	0.0620	0.264
5	0.0494	0.333

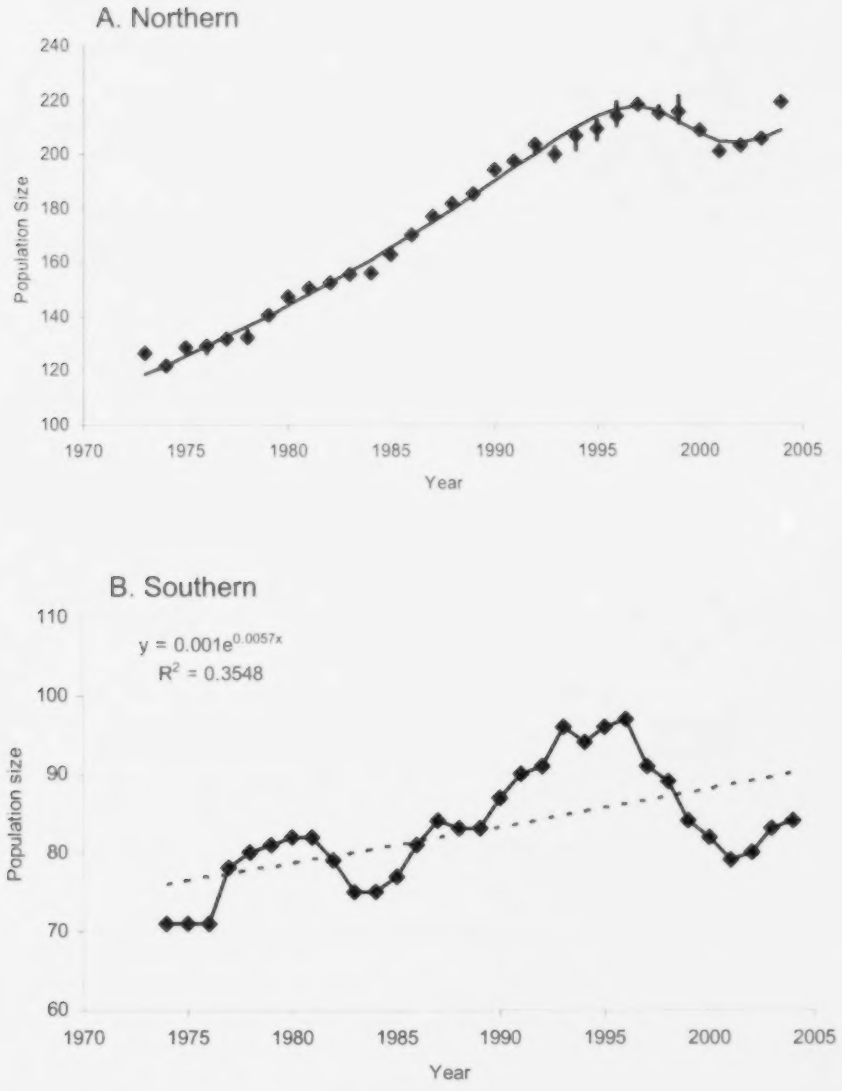

Figure 1. Population size of northern (A) and southern (B) resident communities, 1973-2004.

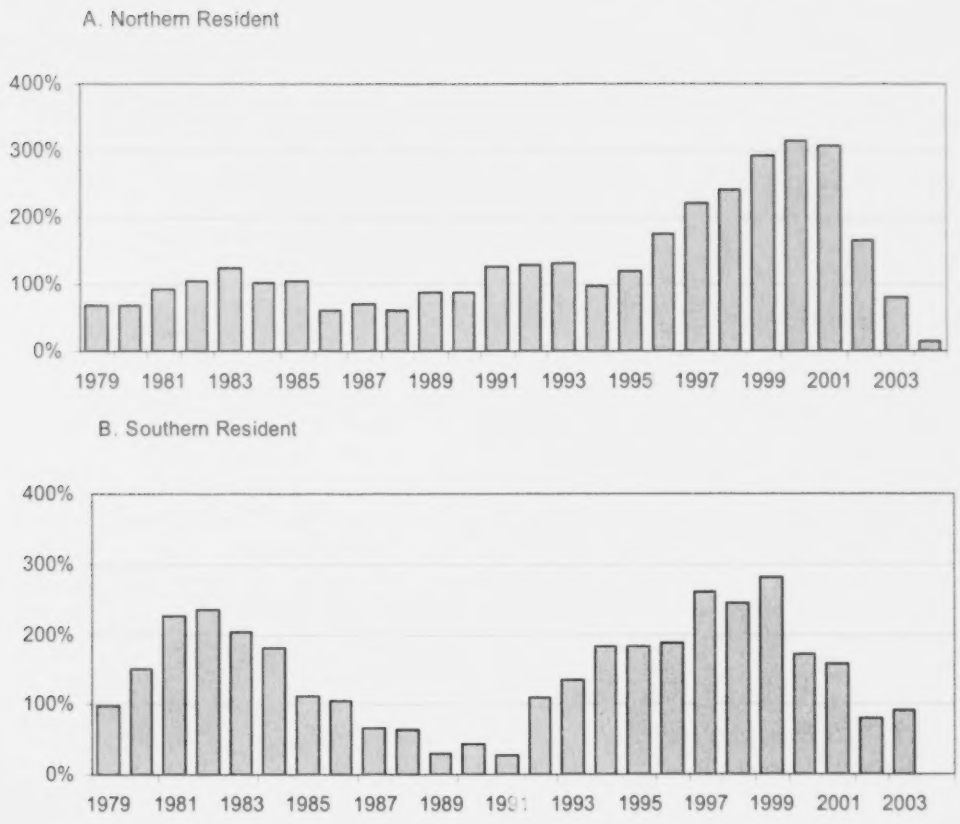

Figure 2. Percentage of expected mortalities observed annually for northern resident (A) and southern resident (B) killer whales, 1979-2004.

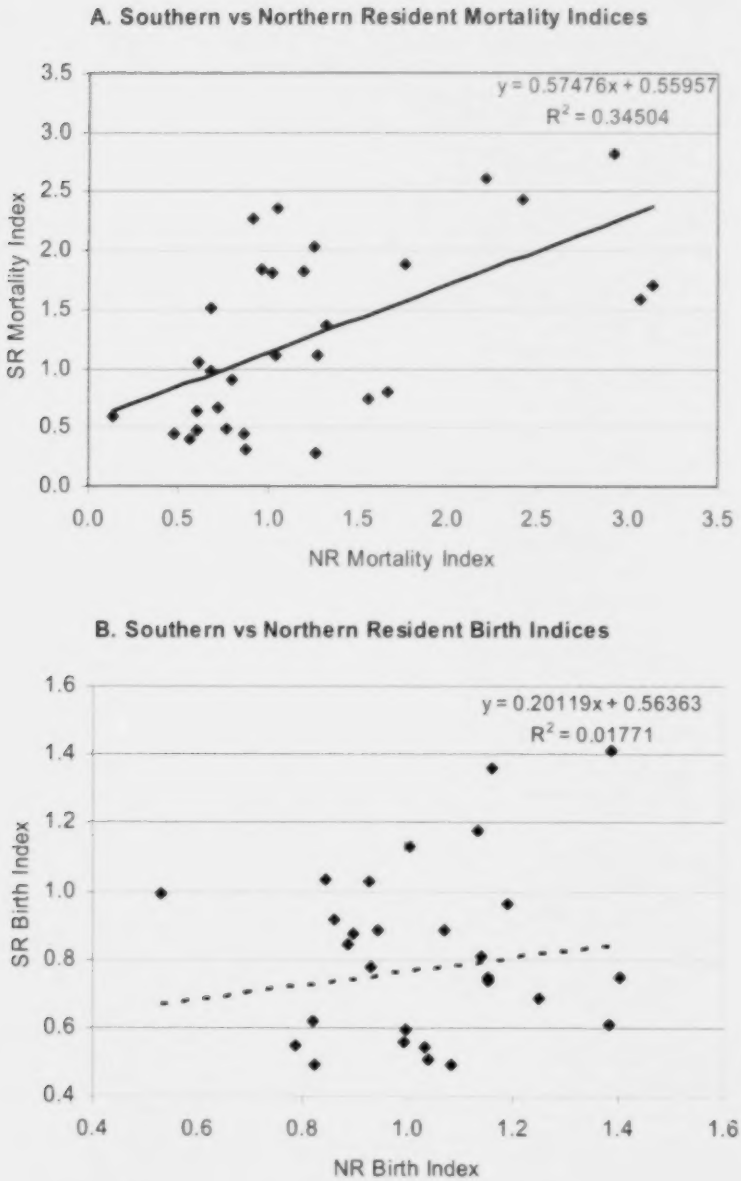

Figure 3. Mortality (A) and birth (B) ratios of southern residents as a function of these indices for northern residents. Mortality ratios are significantly correlated ($P<0.001$), while birth ratios are not.

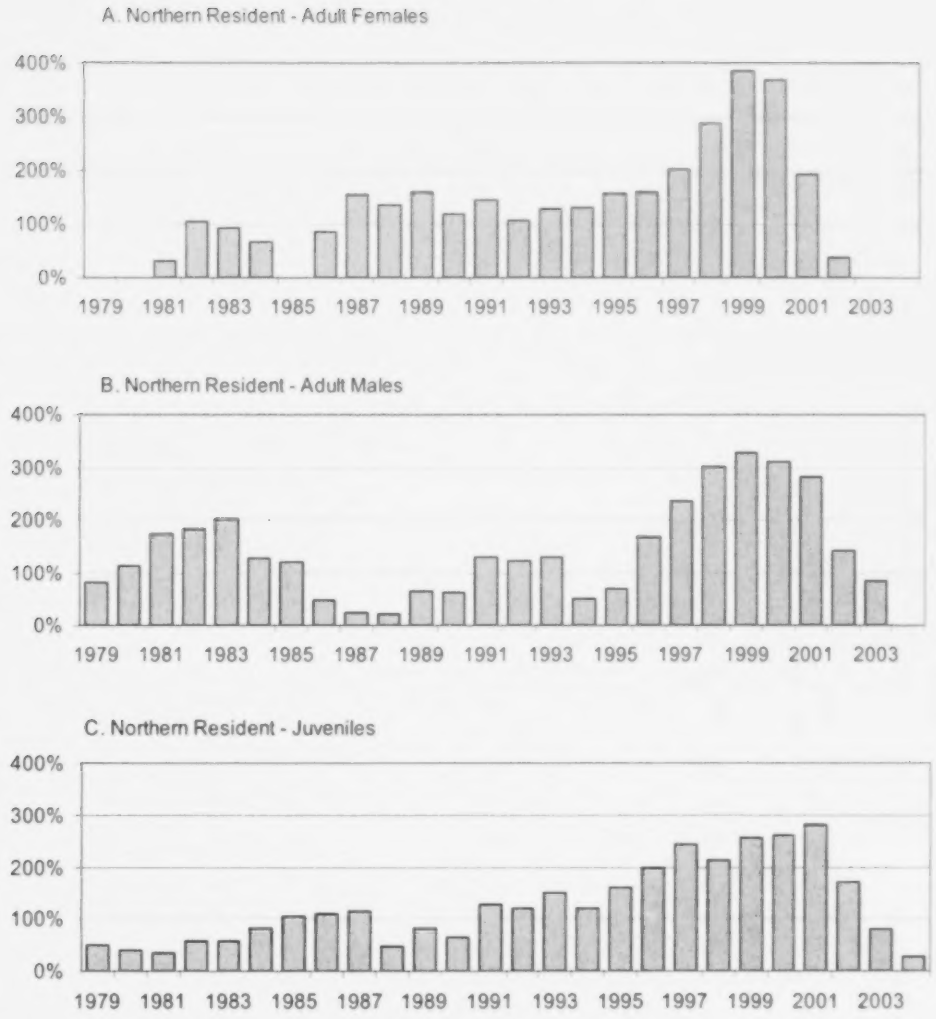

Figure 4. Percentage of expected mortalities observed annually for different age- and sex-classes of northern resident killer whales, 1979-2004.

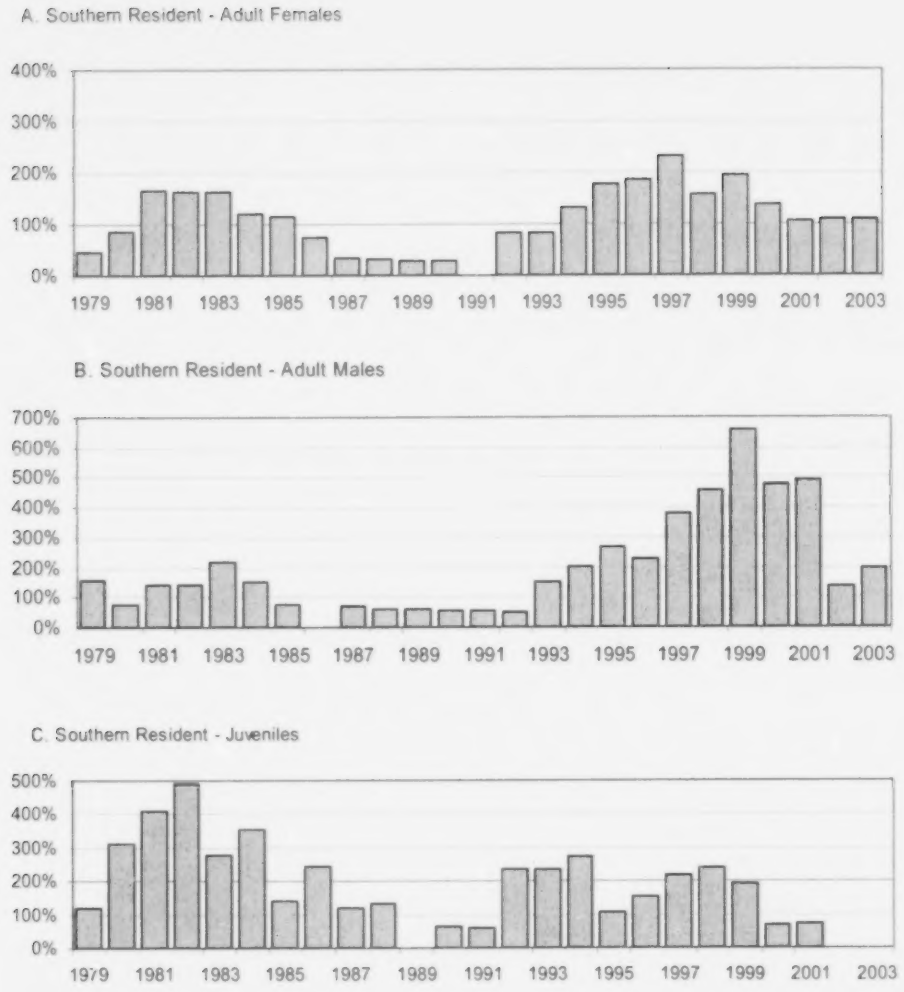

Figure 5. Percentage of expected mortalities observed for different age- and sex-classes of southern resident killer whales, 1979-2004. Note differing scales.

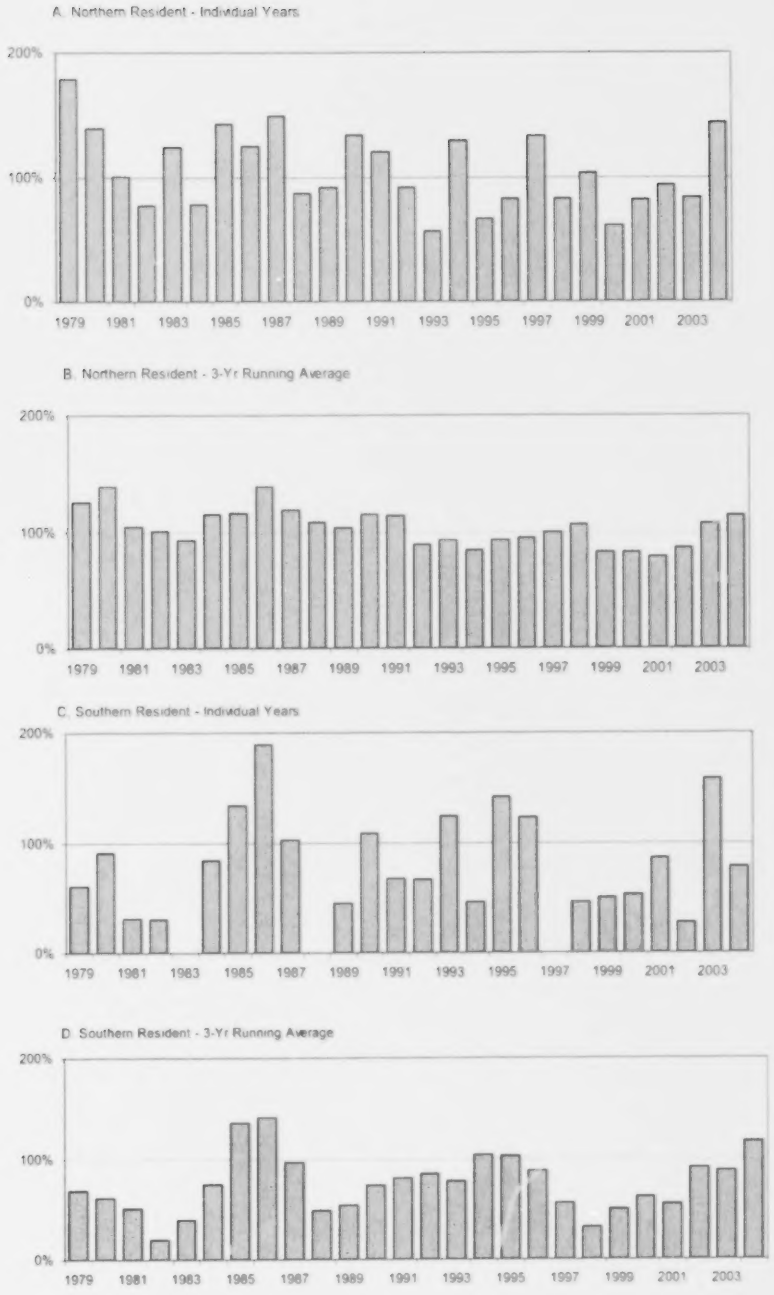

Figure 6. Percentage of expected births observed for northern residents (A = individual years, B = 3-year running average) and southern residents (A = individual years, B = 3-year running average), 1979-2004.

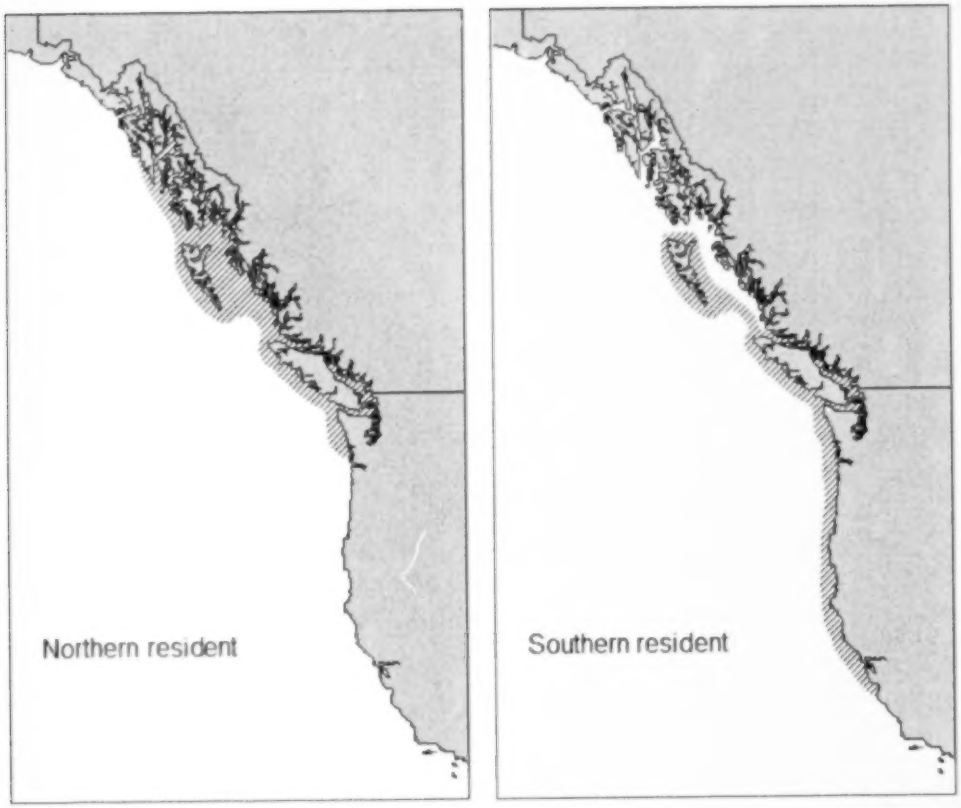

Figure 7. Known geographical ranges of northern (left) and southern (right) resident killer whales. Extent of movement offshore is unknown.

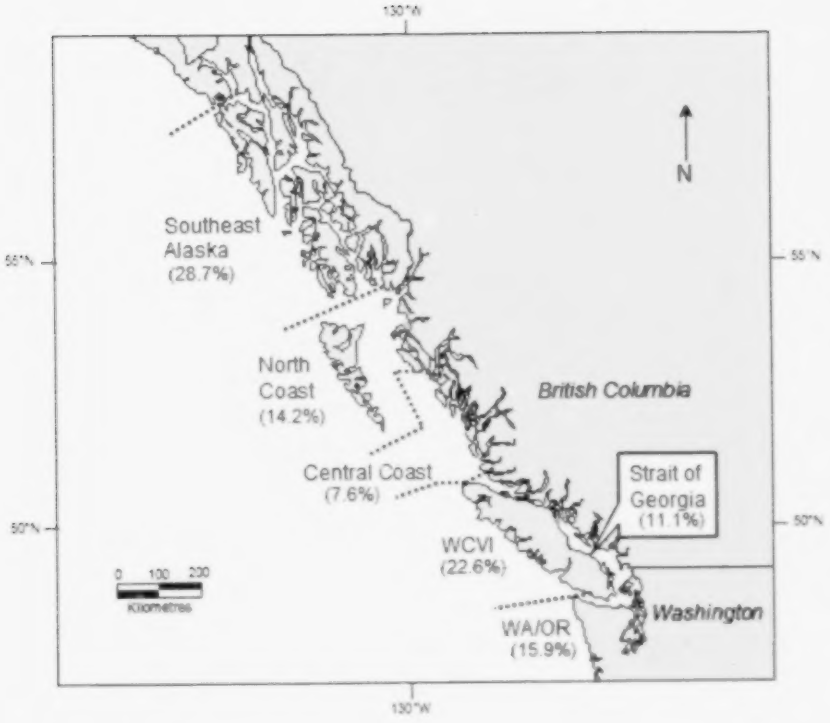

Figure 8. Coastal regions associated with Pacific Salmon Commission chinook salmon abundance estimates, and the proportion (in parentheses) of the total abundance represented by each region. The Washington/Oregon (WA/OR) index area extends beyond the southern margin of this map.

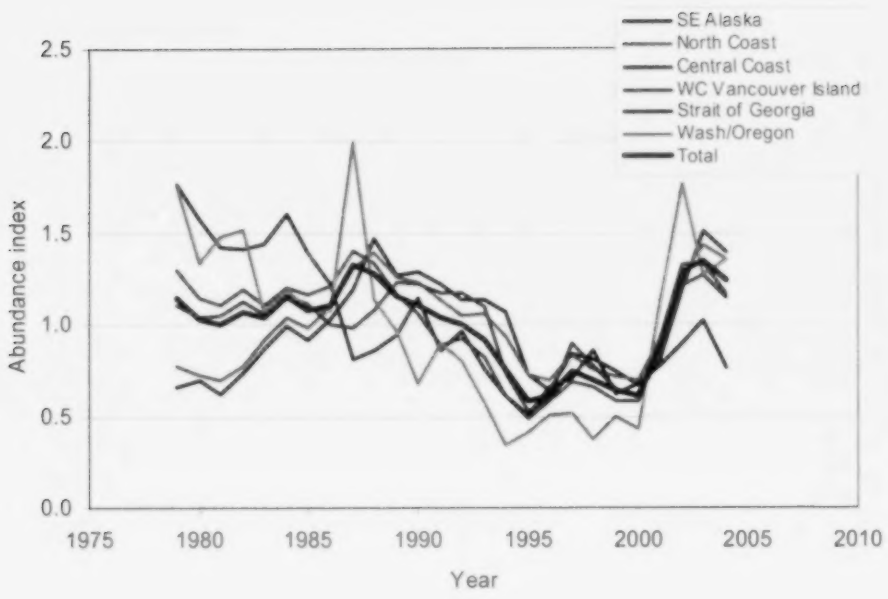

Figure 9. Chinook abundance indices for the 6 west coast index regions, plus the total index for all regions combined, 1979-2004. Indices are derived from abundance estimates by the Pacific Salmon Commission Chinook Technical Committee (see text for details).

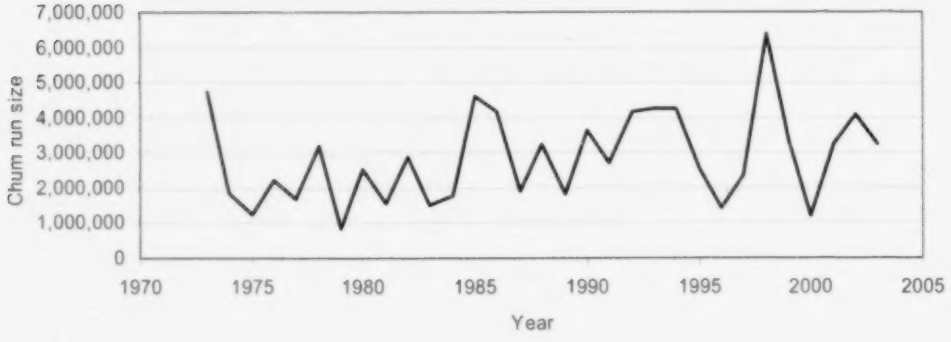

Figure 10. Estimated total abundance (from catch and escapements) of chum stocks in the Inner South Coast Management Area of British Columbia, 1973-2003 (see Ryall et al. 1999, footnote 4 in text).

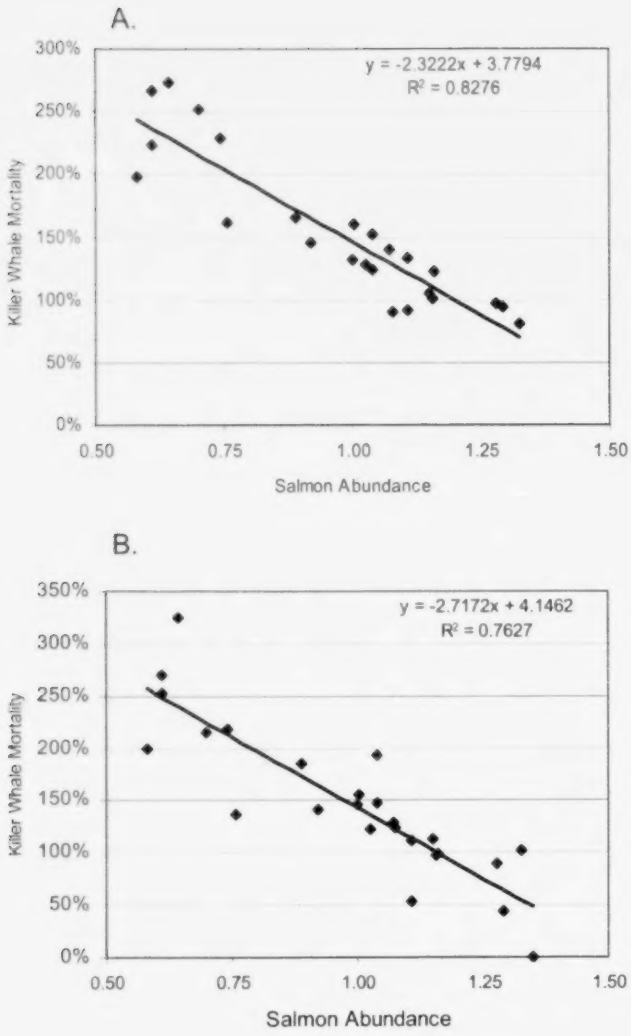

Figure 11. Percentage of expected mortality rates observed in both resident communities combined as a function of total chinook abundance for all British Columbia and southeast Alaska fishery regions, 1979-2004. Mortality deviations are lagged by 1 year after chinook abundance. A = 3-yr running average mortality rates, B = mortality rates for individual years.

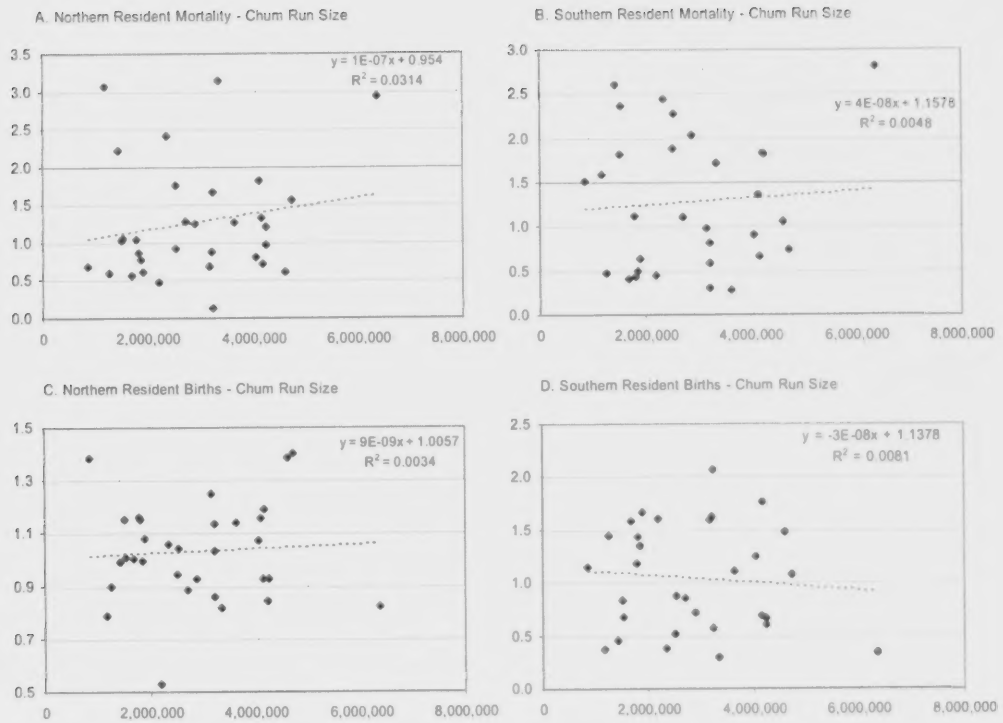
A. Northern Resident Mortality - Chum Run Size
y = 1E-07x + 0.954
R² = 0.0314
B. Southern Resident Mortality - Chum Run Size
y = 4E-08x + 1.1578
R² = 0.0048
C. Northern Resident Births - Chum Run Size
y = 9E-09x + 1.0057
R² = 0.0034
D. Southern Resident Births - Chum Run Size
y = -3E-08x + 1.1378
R² = 0.0081
0
2,000,000
4,000,000
6,000,000
8,000,000

Figure 12. Mortality rates of northern (A) and southern (B) residents, and birth rates of northern (C) and southern (D) residents as a function of chum salmon abundance in the Inner South Coast Management Area. None is significantly correlated.

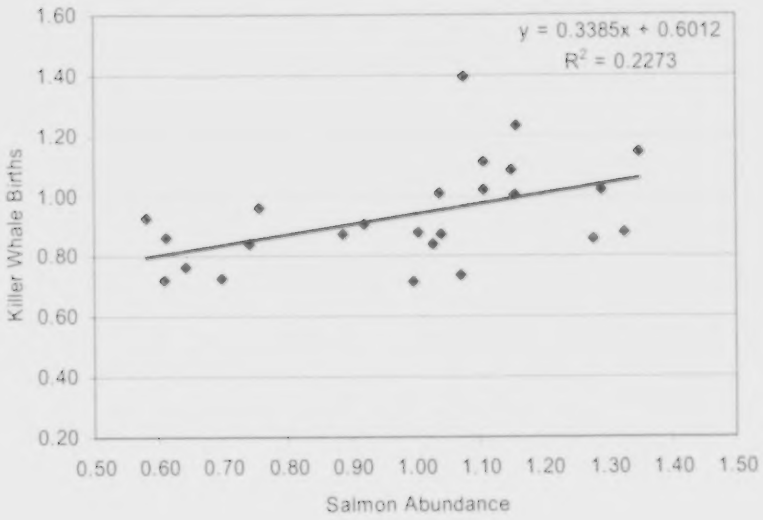

Figure 13. Ratio of observed to expected births for northern and southern residents combined (3-yr running average) as a function of total chinook salmon abundance, all index regions combined, 1980-2004. Birth rate deviations are lagged by 1 year after chinook abundance. ($F_{1,23} = 6.77$, $r^2 = 0.227$, $P < 0.05$)

Appendix 1:

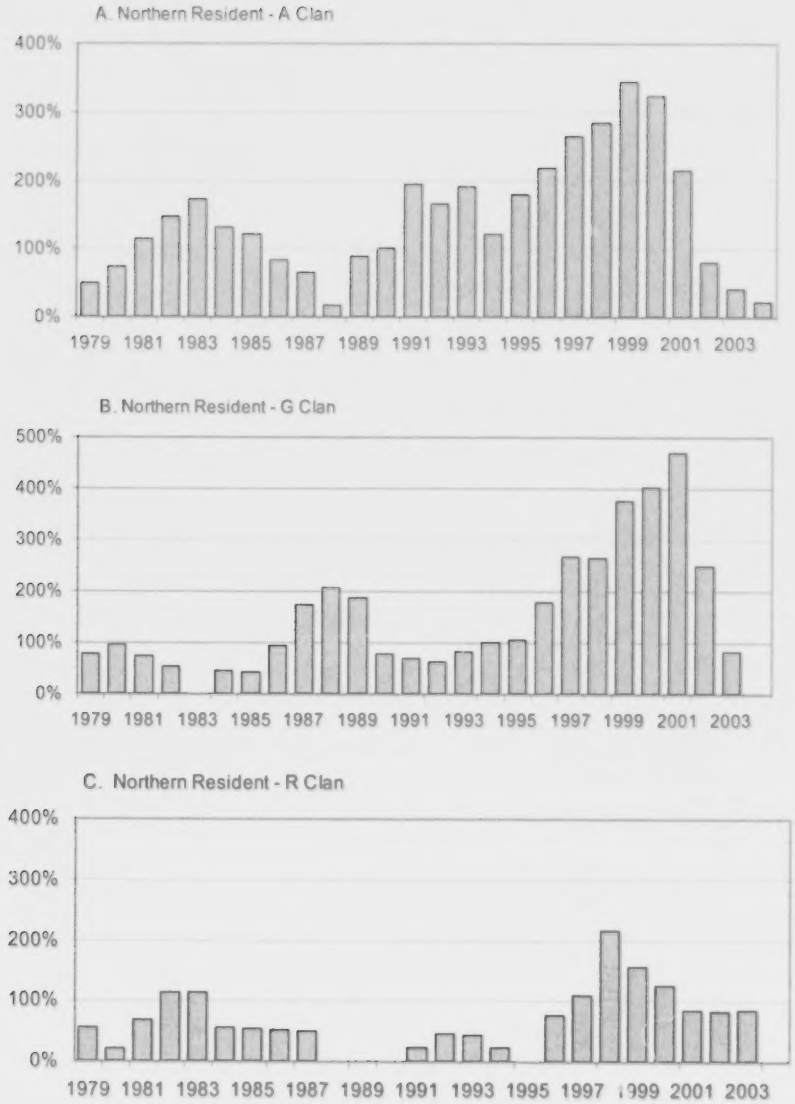

Figure A1. Percentage of expected mortalities observed in A Clan, (A) G Clan (B), and R Clan (C) of the northern resident community, 1979-2004.

Appendix 2:

The relationships between deviations in mortalities and chinook abundance were examined for separate coastal regions. Central Coast and West Coast Vancouver Island regions showed the stronger correlations to mortalities in northern residents than did the North Coast and Southeast Alaska regions. The strongest relationship in northern residents, however, was to all regions combined (Fig. A2). Mortalities in southern residents correlated best with North Coast and Southeast Alaska regions, which was not anticipated due to their more southerly distribution compared to northern residents (Fig. 10). The strength of these correlations results mostly from the high mortality rates seen in southern residents in the early 1980s and the low chinook abundance in these two regions during the same period (Fig. A3).

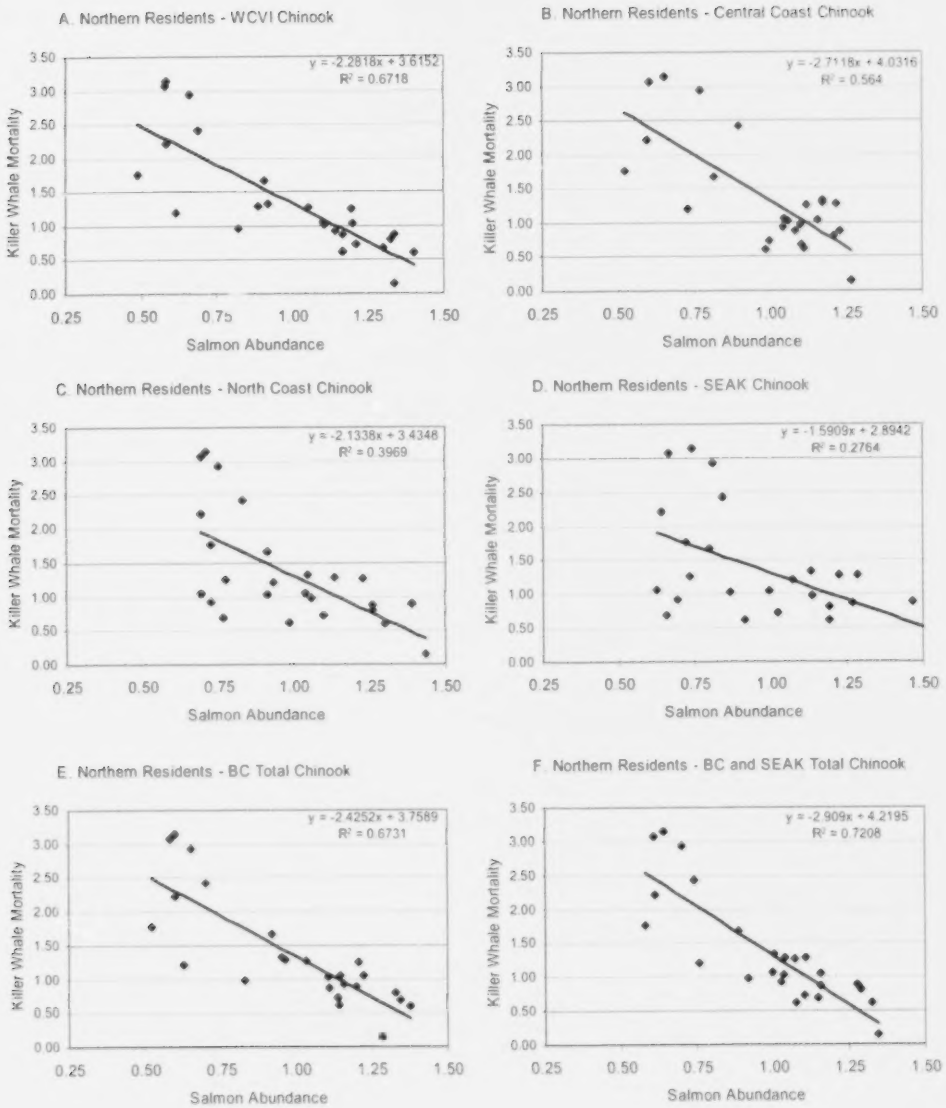

Figure A2. Deviations in mortalities for northern residents as a function of chinook abundance for West Coast Vancouver Island (A), Central Coast (B), North Coast (C), and Southeast Alaska (D) index areas, as well as all BC indices combined (E), and BC and Southeast Alaskan indices combined (F). Mortalities are lagged by 1 year following chinook abundance. All show significant correlations at a level of $P<0.05$ or less.

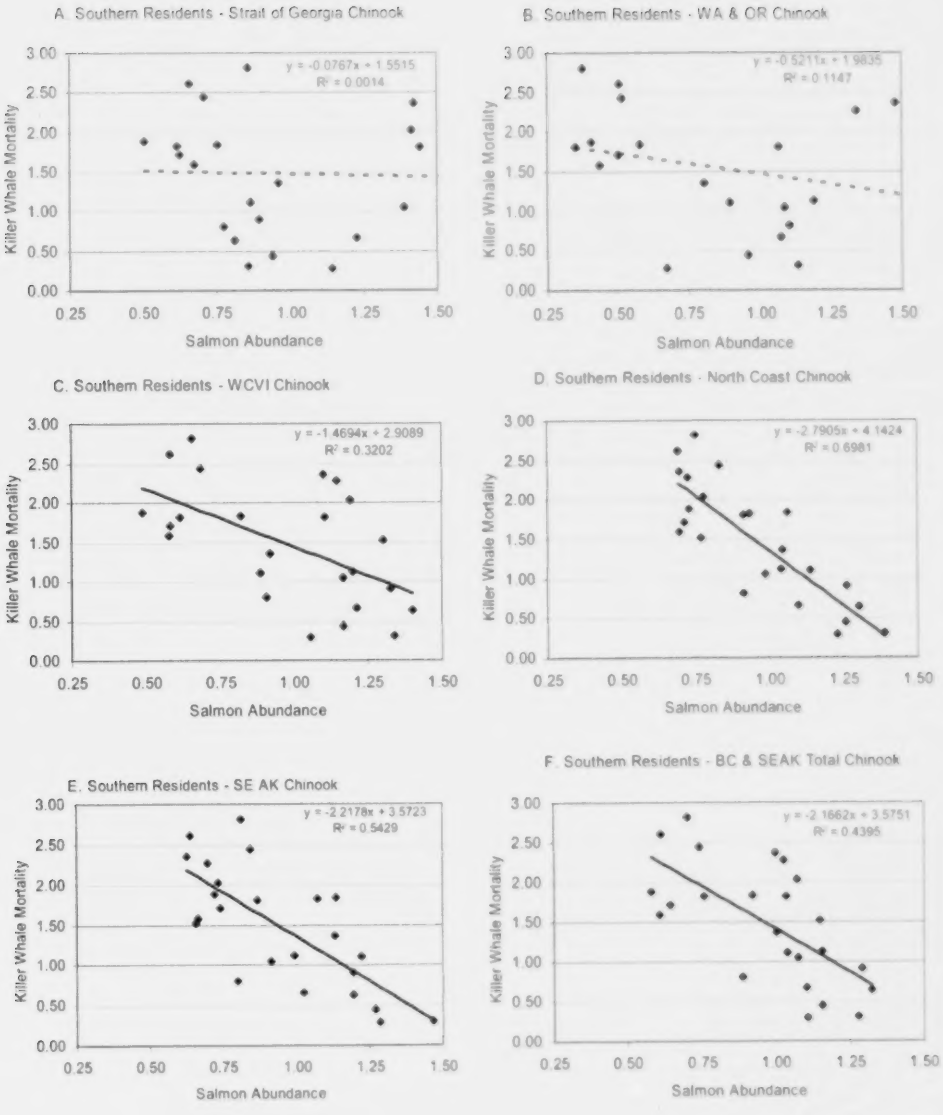

Figure A3. Deviations in mortalities for southern residents as a function of chinook abundance for Strait of Georgia (A), Washington and Oregon (B), West Coast Vancouver Island (C), and North Coast (D) index areas, as well as all BC indices combined (E), and BC and Southeast Alaskan indices combined (F). Mortalities are lagged by 1 year following chinook abundance. All except A and B show significant correlations at a level of $P<0.05$ or less.